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Tolerance and potential for adaptation of a Baltic Sea rockweed under predicted climate change conditions

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ABSTRACT

Climate change is threating species' persistence worldwide. To predict species responses to climate change we need information not just on their environmental tolerance but also on its adaptive potential. We tested how the foundation species of rocky littoral habitats, *Fucus vesiculosus*, responds to combined hyposalinity and warming projected to the Baltic Sea by 2070–2099. We quantified responses of replicated populations originating from the entrance, central, and marginal Baltic regions. Using replicated individuals, we tested for the presence of within-population tolerance variation. Future conditions hampered growth and survival of the central and marginal populations whereas the entrance populations fared well. Further, both the among- and within-population variation in responses to climate change indicated existence of genetic variation in tolerance. Such standing genetic variation provides the raw material necessary for adaptation to a changing environment, which may eventually ensure the persistence of the species in the inner Baltic Sea.

1. Introduction

Climate change is significantly impacting biodiversity and ecosystem functioning worldwide, and by the end of the twenty-first century it may become the most important driver of biodiversity loss and species range shift (Bellard et al., 2012; Poloczanska et al., 2013; Lenoir and Svenning, 2015; Gruner et al., 2016). In the light of the predicted environmental changes, some species may persist by adapting evolutionarily to new conditions but many will shift their distribution with the changing environmental regimes while some may be lost to extinction (Parmesan and Yohe, 2003; Perry et al. 2005; Harley et al., 2012; Poore et al., 2016). The challenge for predicting species responses to climate change is to know their environmental tolerances and, in particular, to understand the adaptive potential of tolerance which may rescue populations from local extinction.

Tolerance to a certain range of environmental conditions determines species' geographical distribution (Levins, 1968; Banta et al., 2012). Although species are often treated as if they responded uniformly to environmental stress (Banta et al., 2012) populations of broadly distributed species experience distinct gradients of abiotic and biotic factors and typically show phenotypic and/or genotypic differences (Sanford and Kelly, 2011; Valladares et al., 2014). The species may adjust its phenotype to the new environmental conditions through phenotypic plasticity (Chevin et al., 2010; Lande, 2014; Valladares et al., 2014). Alternatively, populations may differ in traits related to tolerance, and when such variation exists, some of them may be more prone to extinction in the face of widespread environmental alterations such as climate change (Pearson et al., 2000; Hämmerli and Reusch, 2002; Kelly et al., 2011; Lamichhaney et al., 2012; Stockwell et al., 2003; Berteaux et al., 2004; Reusch et al., 2005). Our understanding of how tolerance, genetic variation of tolerance and phenotypic plasticity may vary among populations and how it affects species responses to changing environment is still in its infancy.

Here we study variation in tolerance to climate change of a broadly distributed brown alga *Fucus vesiculosus* along the environmental gradient in the Baltic Sea. The Baltic Sea is an ecologically marginal habitat for marine species due to its brackish water nature. The inflow of freshwater from many rivers, together with a poor exchange of seawater with the Atlantic, causes a strong salinity gradient, which decreases from approximately 20 PSU (Practical Salinity Unit) in the southwest, in the Kattegat, to 1 PSU in the north (Rönnberg and Bonsdorff, 2004). In addition, the sea surface temperature of the Baltic Sea shows large geographic and seasonal variation. During summer, the temperature exceeds 20 °C, while during winter it might drop below zero (Swedish Environmental Protection Agency, 2001). Climate change is predicted to bring changes in surface seawater temperature, salinity, turbidity, and ice coverage and duration (Meier and Eilola, 2011; Meier et al., 2012). In particular, a rise in seawater temperature and a remarkable drop in salinity are projected for the years 2070–2099 (Meier and Eilola, 2011), with the biggest absolute change in salinity

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occurring in the entrance region.

Fucus vesiculosus (hereafter *Fucus*) is the major perennial macrophyte and foundation species in the Baltic Sea littoral (Wikström and Kautsky, 2007), where it inhabits the shallow hard-bottom areas (Snoeijs, 1999). It plays a key ecological role by forming a highly structured habitat for many epibionts and other associated organisms (Korpinen et al., 2007), thus providing food and shelter to the benthic community (Lotze et al., 2001). The increased surface seawater temperature and decreased salinity expected for the next century may affect *Fucus* populations in the Baltic Sea both directly and indirectly, possibly causing distributional shifts (Leidenberger et al., 2015; reviewed in Takolander et al., 2017a). Warming has been found to impair survival (Wilson et al., 2015) as well as to speed reproductive maturation with decreasing germination success (Maczassek, 2014; Kraufvelin et al., 2012). Warming may also have positive effects on growth of germlings (Steen and Rueness, 2004) or adults, and it may benefit *Fucus* indirectly by reducing grazers (Werner et al., 2015, 2016). On the other hand, some indirect effects of warming such as increased consumption rate of herbivorous isopods (Leidenberger, Harding and Jonsson 2012; Gutow et al., 2016; Rothäusler et al., 2017), changes in quality of the thallus as food (Weinberger et al., 2011), or increase of light-absorbing phytoplankton (Alexandridis et al., 2012) may be harmful for *Fucus*. So far, much less is known about the effects of declining salinity on *Fucus*. Bäck et al. (1992a) showed that Baltic *Fucus* evolved higher tolerance to low salinity than its Atlantic counterpart. Laboratory experiments found that salinities lower than 4 PSU are a physiological boundary for reproductive efficiency of *F. vesiculosus*, and this would therefore limit the distribution of this species (Serrão et al. 1996a, 1999, b). However, *Fucus* individuals have been found in salinity down to 2 PSU in the Bothnian Sea, Gulf of Finland, and the White Sea. This is possibly due to periodic salinity fluctuations during their reproductive period or a localised higher salinity (Ruuskanen and Bäck, 2002; Ardehed et al., 2016). A decrease in salinity between 6 and 3 PSU in the Gulf of Finland was associated with a decrease in thallus size Baltic of *F. vesiculosus* (Ruuskanen et al., 1999).

Even though *F. vesiculosus* experiences different gradients of salinity and temperature across the Baltic Sea, experimental studies seldom account for this interactive effect, and typically only a single environmental factor has been manipulated (Wernberg et al., 2012; Forsman et al., 2016). In the present study, we exposed Baltic *Fucus* to a long-term climate change experiment (140 days) to test if it has the potential to tolerate and adapt to the projected simultaneous summer-time future temperature and salinity conditions expected for the years 2070–2099 in the Baltic Sea (Meier and Eilola, 2011). Based on these climate projections, we tested the following hypotheses: (i) Populations originating from the entrance, central and marginal regions of the Baltic Sea are differently affected by the predicted future conditions of their region: the expected future shift in salinity and temperature for the entrance region can be within the tolerance range but for the populations in the central and marginal regions it may be challenging to tolerate the predicted combination of warming and low salinities. (ii) Populations within regions may vary in their responses to future conditions due to their local differentiation. Such among-population variation represents either geographic genetic variation or phenotypic plasticity in tolerance, both of which may enhance persistence through dispersal from the more tolerant populations. (iii) Populations may harbor within-population variation in tolerance. Also such variation can be based on standing genetic variation or individual variation in phenotypic plasticity. Within population variation indicates potential for adaptive responses to climate change. Given the important role of Baltic *Fucus*, this information is essential in evaluating the consequences of global climate change on rocky littoral communities within this basin.

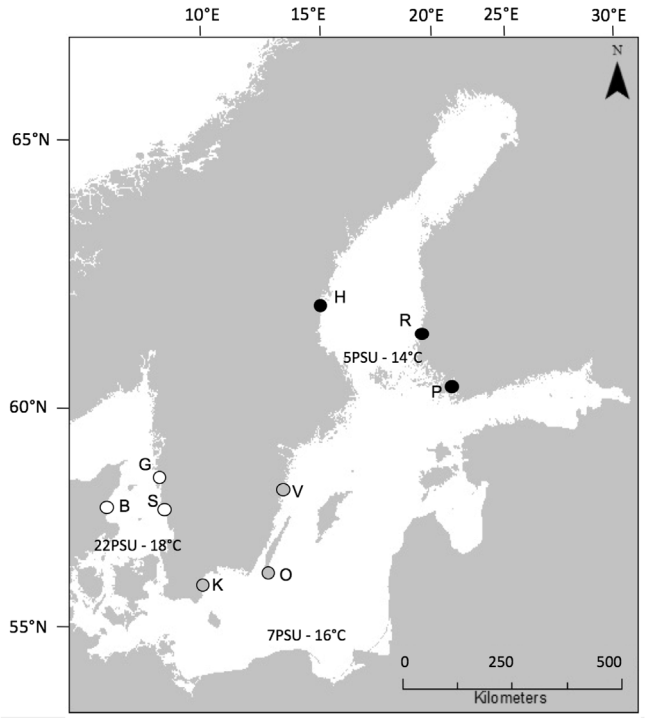

Fig. 1. Location of *Fucus* sampling sites in the marginal (black dots: H, R, and P), central (grey dots: V, O, and K) and entrance (white dots: S, B, and G) regions. Summertime (average values from June to August) sea surface salinities and temperatures for each Baltic region are indicated as average values for years 1990–2008, obtained from Siegel et al. (2008). Different letters denote the different populations sampled within a region.

2. Materials and methods

2.1. Sampling of Fucus

We collected *Fucus vesiculosus* from three different regions – entrance, central, and marginal – of the Baltic Sea (Fig. 1, Table 2) in summer 2014. Within each of these region, we randomly sampled three populations, and from each population we collected 25 individuals. Herein, one individual is defined as all the apical tips of a thallus growing from a single stem attached to a holdfast. We detached the individual in at least 5 m distance between each other to ensure the uniqueness of samples (see Supporting Information for more details). We only genotyped two populations from the marginal region where clonality has been previously recorded to ensure that they were different genotypes (for the analyses see Tables S1, S2 and S3). For the rest of the populations (from the entrance and central regions), the distance between samples collected and the fact that we were detaching only one stem from one holdfast ensured the uniqueness of the genotypes. Individuals were collected by snorkeling and at all sites they were detached in the range between 0.5 and 2 m depth.

From 27th to 28th June 2014, we collected the marginal populations, while the central populations were gathered between the 2nd and 3rd of July. On the 3rd and 4th of July, we collected the entrance populations. All individuals were kept in coolers between wet paper tissues to avoid dehydration and transported to the Archipelago Research Institute (University of Turku) at Seili (60° 14′ N, 21° 58' E), where they were carefully rinsed with freshwater to remove associated grazers and epiphytes. Then, we stored the algal individuals in their native salinities until the experiment started.

2.2. Fucus preparation for the experiment

Once our sampling was complete we split each algal individual (N = 25 per population and region) into eight similar sized branches

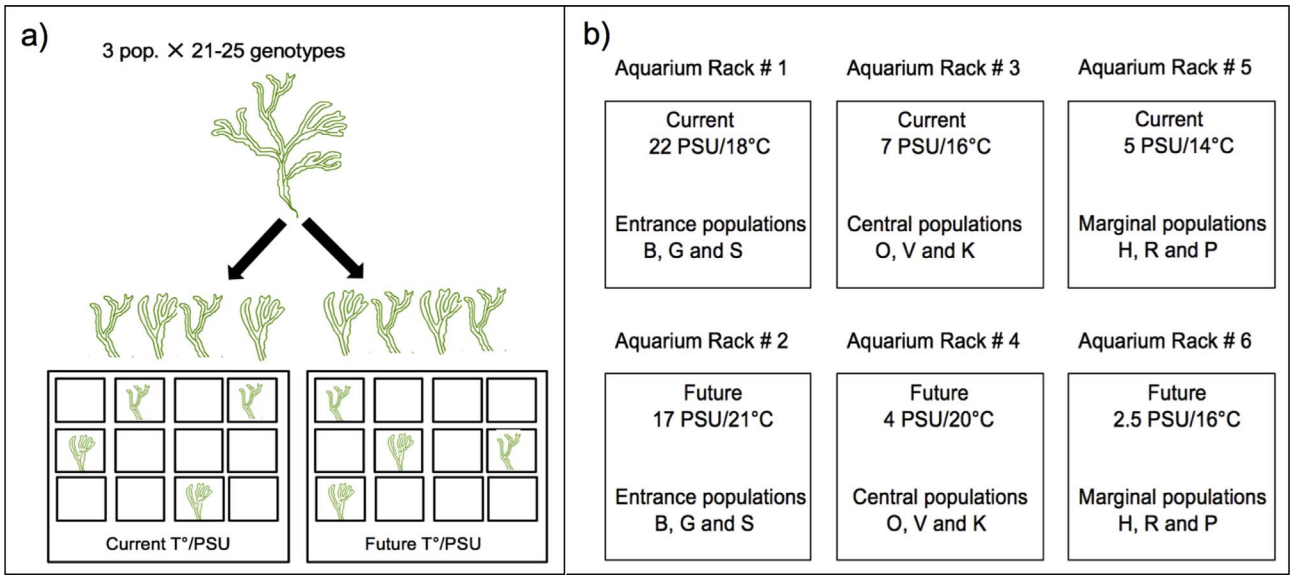

Fig. 2. Schematic illustration of the experimental design. Fig. 2a. Schematic of the experimental design, detail about pseudo-replication of each genotype in multiple ramets. Fig. 2b shows how we distributed each population in the aquarium racks.

(we hereafter refer to one branch as a ramet - initial length, mean ± SE: 7.1 ± 0.05 cm; initial # of apical meristems: 8.7 ± 0.16; initial wet weight (WW): 0.99 ± 0.02 g). Four of the branches were distributed randomly among the aquaria in the current conditions, and the other four among the aquaria in the future conditions, so that each aquarium contained a mix of 25 ramets (Fig. 2a). Epiphytes were rinsed from experimental algae when necessary to avoid competition for nutrient availability and light. Micro-environmental effects were accounted for by randomly relocating the algae within each aquarium each week. In order to avoid flotation of the ramets, a small ceramic weight was attached individually with a cable tie to each ramet. To prevent any damage, we fixed a piece of a plastic mat between the cable tie and the ramet. We first started to prepare the marginal populations (11th and 12th of July), then the central populations (12th and 13th July) and finally the entrance populations (15th and 16th of July).

At the starting point all aquaria were set up with current conditions. After all the ramets have been introduced in their respective aquaria racks, we simultaneously shifted the temperature and salinity of all future aquaria within one day. The experiment started for all populations on the 23rd of July and ended on 10th of December.

2.3. Experimental setup

We examined the effects of different temperature and salinity conditions on the performance of *Fucus* in an indoor aquarium experiment. Because climate change typically involves simultaneous shifts in several abiotic factors (IPCC Climate Change, 2007), we focused on the combined effects of hyposalinity and increased temperature. These are the main environmental factors that determine the structural and functional characteristics of aquatic biota, and they covary regionally, both currently and in the future projections.

We used six aquarium racks (each consisted of 12 aquaria) to expose, separately, the algal material from each region to two different climate conditions, the current and predicted future (Table 1, Fig. 2b). We used summer conditions because during this period *Fucus'* growth rate is up to three times faster than in the winter (Lehvo et al., 2001). We extended the duration of the experiment further than the natural duration of the Baltic summer to detect the long-term influence of the future conditions. The long term exposure to hyposalinity/warming may evidence patterns of among- and/or within population variation in performance that may not be evidenced by short term experiments. In order to apply a realistic setup, the current conditions within each region were based on the average summertime salinity and temperature conditions of the sampling sites within the three regions (Table 2). The data on future (2070–2099) changes in summer salinity and temperature for Baltic coastal areas come from the model RCAO-ECHAM-A2-REF from Meier and Eilola (2011). The data on current surface seawater temperature and surface salinity have been averaged from the mean values for June to August for each region (http://www.balticnest.org/).

Each aquarium rack consisted of a bottom tank (~300 L) and 12 aquaria (24 L each), which were connected to each other via recirculating water system. Seawater was pumped from the bottom tank individually to each aquarium, from where it flowed back into the

Table 1
Average summer sea surface temperature (SST) and salinity (SSS) for current and future conditions within the three regions. Current conditions were calculated by averaging the monthly means from June to August obtained from the Baltic Nest Institute (http://www.balticnest.org). The future expected conditions were set according to the model of Meier et al. (2012).

Region	Current		Future	
	SSS (PSU)	SST (C°)	SSS (PSU)	SST (C°)
Entrance	22	18	17	21
Central	7	16	4	20
Marginal	5	14	2.5	16

Table 2
Seawater surface salinity (SSS, Feistel et al., 2010) and seawater surface temperature (SST, Siegel et al., 2008) (mean ± SD) for the summer period (June to August). Salinity and temperature means for each site were averaged for observations from open water and coastal areas for the regions targeted by our sampling. The number of individuals sampled for each population is corrected after the genotyping.

Region	Population	Coordinates (N, E)	SSS (PSU)	SST (°C)	# Individuals
Entrance	B	56°31′, 10°38′	23 ± 11	17 ± 3	25
Entrance	G	57°07′, 12°12′	24 ± 7	17 ± 3	25
Entrance	S	56°19′, 12°45′	24 ± 7	17 ± 3	25
Central	O	56°11′, 16°23′	7.3 ± 2.5	16 ± 4	25
Central	V	57°41′, 16°43′	6.8 ± 1.5	17 ± 4	25
Central	K	55°41′, 14°13′	7.7 ± 2.5	16 ± 3	25
Marginal	H	61°41′, 17°31′	5 ± 3	13 ± 3	21
Marginal	R	61°08, 21°18′	5.5 ± 3	13 ± 3	23
Marginal	P	60°08′, 22°17′	6.3 ± 3.5	15 ± 2	25

bottom tank. Before it was pumped up, the seawater was cleaned first by an acrylic filtration unit (SCHURAN Jetskim 120) equipped with a mechanical and biological filter, then by a protein skimmer, and finally by UV radiation. To regulate the desired water temperature, each bottom tank was equipped with a chiller/heater. We obtained the region-specific water salinities for both climate conditions (current and future) by adding artificial sea salt to seawater or by dilution with distilled water. To ensure ample nutrient availability, we added 3 g of Osmocote® controlled-release fertilizer (NPK 15-9-12 + 2MgO + trace elements, 2 months) to each rack at the start of the experiment and every second month.

Each shelf contained four aquaria, which received artificial light from two LED lamps (Radion ™ XR30w Pro lamp). We used a 17:7 h light:dark rhythm, which was similar to the average summer light conditions in the Baltic Sea. The light level slowly increased in the mornings, reached a maximum intensity (1200 μmol m^{-2} S^{-1}) at the aquarium water surface between 11:00 and 14:00, and then slowly decreased in the evenings to darkness.

During the experiment, we kept the water level and salinity in the aquarium system constant by adding ion-exchanged water. We monitored temperature (daily) and salinity (weekly) to ensure that conditions remained at the desired levels (Table 1). We also measured pH weekly to ensure it stayed within the natural range of the Baltic Sea (mean ± SE: 8.31 ± 0.07).

2.4. Measuring responses

We measured the growth rate and survival of *Fucus* as a proxy for sensitivity to environmental changes, since they are dependent on the ratio between respiration and photosynthetic activity and they give an overall estimate of the algal performance (Karsten, 2008). Growth rate was measured as a change in wet biomass (g WW), in length along the major axis (cm), and in the number of apical meristems during the 140 d experiment. Therefore, each ramet was measured at the beginning and at the end of the experiment. For the growth rate in terms of biomass, we gently dried the ramets between paper tissues before determining their initial and final weight. As there was mortality during the experiment, the growth measures refer to growth of the survivors after 140 days. Therefore, we measured the growth rate of the most tolerant individuals. As the different growth rate measures lead to similar conclusions, we present here only the biomass gain rate (expressed as g WW/140 d), but give the summary data and analyses for the length and meristem gain rate in supplementary material (Figure S1, S2 and S3, Tables S4–S5).

We recorded survival throughout the experiment and at the end. We checked the ramets weekly and defined as dead those with > 90% of the thallus area showing necrosis. When an individual started to degenerate, > 90% necrosis typically proceeded relatively quickly, between the weekly observations. Survivors didn't show dead thallus parts. Survival was expressed as the probability of being alive at the end of the experiment. Growth rate and the survival probability of each individual was calculated as the average of N = 4 ramets in the future and N = 4 ramets in the current conditions. These means were calculated using the Glimmix procedure as the 'best linear unbiased predictors' (BLUPs), which are considered the best estimates for random factors (Robinson, 2008).

2.5. Statistical analysis

We analyzed the variation in growth rate (length, number of apical meristems, and biomass) using a general linear mixed model within populations separately for each region. A normal distribution was used for the error variance, and the analyses were implemented using the procedure GLIMMIX in SAS 9.4 (SAS Institute Inc., 2013). The fixed factor in the model was climate change (future and current conditions). Random factors were population, individual within population, aquarium, and all the possible interactions between these factors and climate change. The aquarium was included as a random factor to capture possible variations in growing conditions among aquaria within a rack (e.g. lighting, position effect, water through-flow). In the analyses of growth rate, we used the initial size as a covariate and tested all of its interactions with the fixed factor. We then simplified the model by removing non-significant effects, starting from the higher-order interactions, with the aid of the Akaike Information Criterion (AIC). The significance of fixed effects was tested using F-statistics, with the denominator degrees of freedom estimated by the use of the Kenward-Roger approximation (Kenward and Roger, 1997). The significance of the random effects and the random-by-fixed effect interactions was tested by X^2-tests of the differences in the 2 × log likelihood value of that factor included versus excluded from the model (likelihood ratio test, Littell et al., 2006).

The survival probability (after 140 days) was analyzed using a generalized linear mixed model, with survival as a binary response variable (alive, dead). This model was similar to that described above for the growth rate analyses.

3. Results

3.1. Growth performance among regions under climate change conditions

Populations originating from different regions varied in their biomass gain in the current conditions of their respective region: entrance populations grew the most, followed by the central and marginal populations (Fig. 2). The entrance populations tolerated the future conditions well: there was no overall difference in biomass gain between current and future conditions (Fig. 3, Table 3). In contrast, future conditions were harsh for the central region populations that grew less compared to their counterparts in the current conditions (Fig. 3, Table 3). Similarly, biomass gain of the populations from the marginal region was strongly hampered by the future conditions (Fig. 3, Table 3).

3.2. Variation among populations and individuals in growth responses to climate change

Within the entrance region, the biomass response to climate change varied among populations (Fig. 3, Table 3). Algae from the population G tolerated the future conditions the best, gaining similar amounts of biomass in both climate conditions, while for the populations B and S, the difference between climate conditions was more pronounced (25% and 16% respectively; Fig. 3). In the central region, we found no differences among populations in their biomass response to climate change, but, in the marginal region, we found such variation (Fig. 3, Table 3): The population R was the least tolerant to climate change and grew 98% less when exposed to future conditions, while the decrease in growth in future conditions was 80% for the population P and 70% for the population H.

We found pronounced among-individual variation in biomass gain in entrance and marginal populations as indicated by the significant among-individual variance component (Table 3). Most interestingly, individuals in the central populations varied in their growth response to climate change (Fig. 4, Table 3) indicating that different individuals expressed varying tolerance to future conditions. It is worth to note that the despite the among-individual variation in tolerance remained also the after strong mortality selection during the experiment (similar among-individual variance in both the climate change conditions in Fig. 4).

3.3. Effects of future climate change conditions on survival of Fucus across the Baltic Sea regions

Fucus originating from the entrance region survived well in both the current and future conditions indicating high tolerance to future

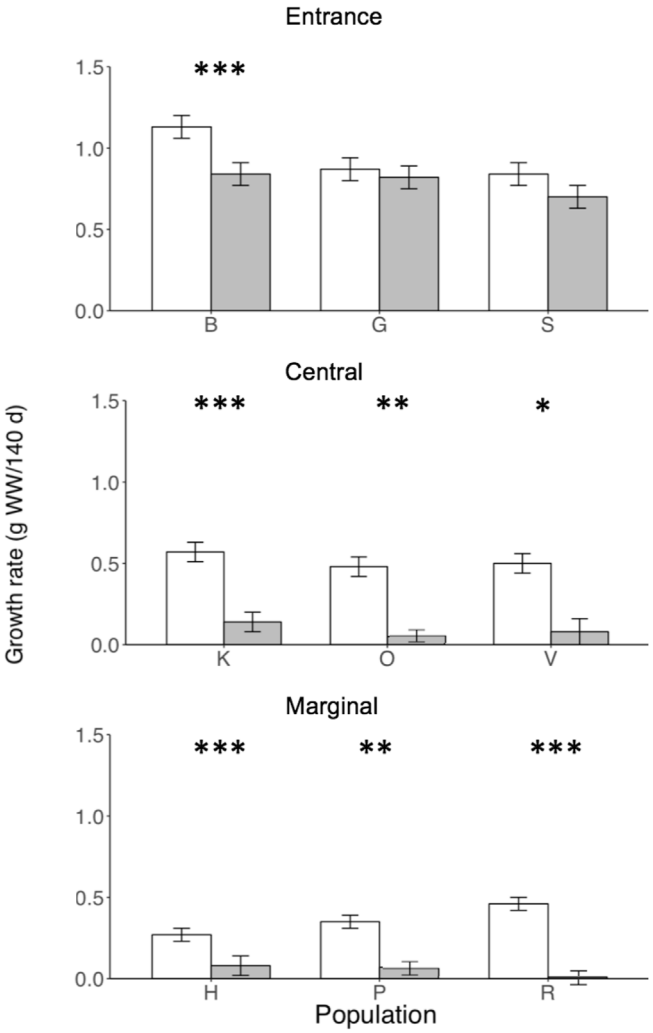

Fig. 3. Growth rate (g WW/140 d, mean ± SE, adjusted for the average initial size of algae) for *Fucus* populations in current and future conditions displayed by region. The biomass gain of each population is based on the individual estimate of each survivor. The number of individuals was N = 25 for every population except for H (N = 21) and R (N = 23) The identity of each population is indicated on the x-axis. Asterisks above denote the degree of significance indicated by the general linear model (*p < .05, **p < .01, ***p < .001).

conditions (Fig. 5, Table 4). Instead, survival of *Fucus* originating from the central region and even more that from the marginal region was hampered by their future conditions (Fig. 5, Table 4). Only 34% of

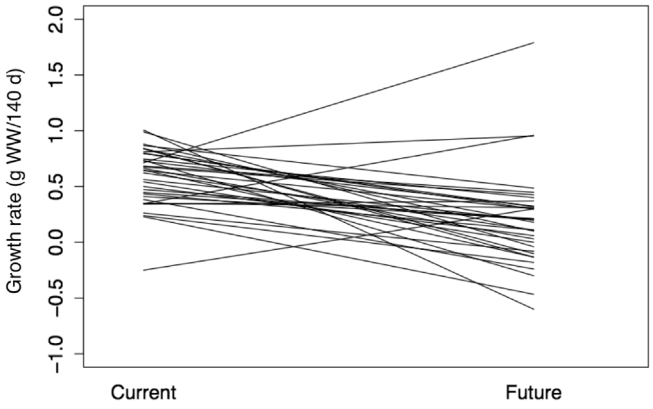

Fig. 4. Individual estimates for growth rate (g WW/140d) in current and future conditions for the central populations. Lines connect the average of each individual (N = 35) in the two conditions. The individual average was calculated averaging 1to 4 ramets for each condition.

Fucus ramets from the central region and 23% from the marginal region survived until the end of the experiment in the future conditions.

Marginal populations varied in their survival responses to climate change (Fig. 5, population-by-climate change interaction in Table 4). Furthermore, within the marginal populations individuals responded differently to climate change (individual-by-climate change interaction in Table 4). Individuals within entrance and central regions varied in their survival but not in their survival response to climate change (Table 4).

4. Discussion

4.1. Climate change effects on algal growth and survival

Our results show that the tolerance of *Fucus* populations to their projected future conditions varies along the Baltic Sea. Populations from the entrance region tolerated future conditions well, maintaining their growth and survival unchanged between current and future conditions. This suggests that their future hyposalinity and warming is within the current range of tolerance of the populations at the Baltic Sea entrance. Instead, future climate conditions had a pronounced negative effect on survival of populations from the central region and an even a more severe impact on those from the marginal region. Moreover, the growth reduced to about fifth of that in the current conditions in populations from the central region, and almost completely ceased in the marginal ones. We suggest that while the populations at the Baltic Sea entrance are likely to tolerate well the future conditions, those from the central and marginal regions of the Baltic Sea are faced with serious challenges and are unlikely to persist in the current distributional range

Table 3
Results from general linear mixed models that tested the fixed effects of climate change and the random effects of population, individual, and aquarium on biomass gain for each region. Initial size was used as a covariate in the analyses.

Source of variation	Entrance			Central			Marginal		
	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P
Fixed Factors									
Cl. change	1, 2.82	3.1	.18	1, 43	42.8	< .001	1, 4.4	15.2	< .05
In. size	1, 472	113	< .001	1, 311	0.19	.67	1, 321	12.9	< .001
In. size × Cl. Change									
		χ^2	P		χ^2	P		χ2	P
Random Factors									
Population		0.52	.24		0.86	.35		–	1
Individual		18.8	< .001		0.01	.91		40.6	< .001
Population × Cl. Change		5.12	< .05		–	1		18.9	< .001
Individual × Cl. Change		0.47	.25		8.24	< .01		–	1
Aquarium		7.71	< .05		–	1		0.5	.48

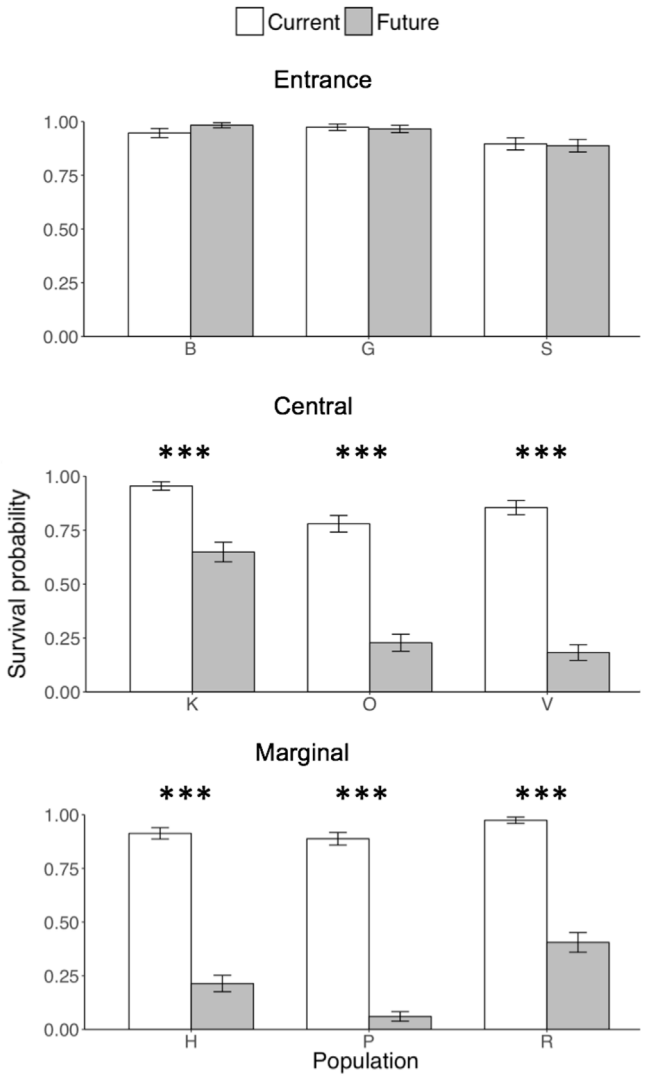

Fig. 5. Survival estimates (mean ± SE) for *Fucus* populations after 140 days in current and future conditions, separately by region. The survival of each population is based on the individual estimate, obtained from the average of N = 4 ramets for each condition. The number of individuals was N = 25 for every population except for H (N = 21) and R (N = 23).

unless their tolerance cannot adapt evolutionarily with the environmental change.

The negative effects of low salinity on seaweed performance have been attributed to the inability to maintain osmotic balance (cell turgor pressure) and to keep a positive ratio between photosynthesis and respiration (Hellebust, 1976). Low salinity (≤2 PSU) is known, for instance, to damage the cellular structures responsible for protein synthesis and energy metabolism (Tropin et al., 2003). Low mannitol contents have been found in response to low salinity and combination of high temperature and hyposalinity in *F. vesiculosus* (Munda and Kremer, 1977; Takolander et al., 2017b), as this compound is also used for osmoregulation (Groisillier et al., 2014; Munda and Kremer, 1977). Negative effects of hyposalinity on *Fucus* growth have been found in experimental studies. For instance, Bäck et al. (1992b) showed that Baltic *Fucus* from the marginal region in the Gulf of Finland could grow and survive in salinities from 6 to 12 PSU, but that salinity extremes (1.5, 34, and 45 PSU) reduced both growth and survival. *Fucus* from the marginal region has also been reported to tolerate short-term (26 h) exposure to hyposalinity (2.5 PSU) without any signs of photoinhibition or damage to the photosynthetic machinery (Rothäusler et al., 2016). Moreover, there is also evidence on local adaptation to local salinity (Johansson et al., 2017): a reciprocal transplant experiment indicated that *F. vesiculosus* from the Atlantic and Baltic Sea grows better in their local than in foreign salinity (respectively 24 and 4 PSU). However, Serrão et al. (1996b) showed that sperm motility and fertilization success of *F. vesiculosus* decreases sharply in salinity below 5PSU, suggesting that early life stages might be most important for the persistence of the species at extremely low salinity.

Temperature plays an important role in algal physiology because it controls the photosynthetic rate (Raven and Geider, 1988), which affects the rate of carbon fixation by RuBisCO (Sukenik et al., 1987). Warming temperatures become stressful for plants when they affect the balance between protein denaturation and the action of heat-shock proteins and the higher production of proteins (Csikász-Nagy and Soyer, 2008). Moderately warm temperatures enhanced growth in *Ascophyllum nodosum* (Keser et al., 2005) and *F. vesiculosus* from the western Baltic Sea where it grew and survived well in temperatures ranging from 5 to 26 °C, with a damaging effect on the photosynthetic system only at temperatures > 26 °C (Graiff et al., 2015). A similar result was reported for eastern Atlantic populations of *F. vesiculosus* (Russell, 1987), in which high water temperature affected the sensitivity of the photosynthetic machinery. However, Al-Janabi et al. (2016) found that the effects of temperature changes on Baltic *Fucus* germlings depend on the season: a 5 °C increase in natural temperature enhanced the growth in early summer, but it caused a severe mortality in late summer. Warming may also be responsible for temporal changes in receptacle maturation such as shown for *F. vesiculosus*, under experimental conditions (Graiff et al., 2017) but also *in situ* (Kraufvelin et al., 2012). Indeed, if warming will increase the duration of the reproductive period of *Fucus*, it is possible that enhanced window for recruitment may help buffering the losses caused by hyposalinity/warming, at least in the regions where low salinity is not limiting fertilization.

Because climate change modifies several abiotic factors simultaneously, we designed our experiment to detect only the combined effect of the predicted future temperature and salinity combinations in the Baltic Sea, not to separate the single factor effects. The combined effect

Table 4
Generalised mixed model statistics for the probability of survival at 140 days, displayed separately by region.

Source of variation	Entrance			Central			Marginal		
	ndf, ddf	F	P	ndf, ddf	F	P	ndf, ddf	F	P
Fixed Factors									
Cl. change	1, 2	0.14	.74	1, 2	62.4	< .05	1, 2	90.7	< .05
		χ^2	**P**		χ^2	**P**		χ^2	**P**
Random Factors									
Population		1.31	.25		1.85	.16		0.55	.46
Individual		4.83	< .05		60.7	< .001		0.74	.4
Population × Cl. Change		–	1		1.18	.27		3.40	< .01
Individual × Cl. Change		–	1		–	1		31.9	< .001
Aquarium		–	1		–	1		–	1

of future seawater salinity and temperature may be simply additive, or it may involve antagonistic or synergistic interactive effects. A meta-analysis of multi-stressor studies by Wahl et al. (2011) found that for *Fucus* spp. the combined effects were on average additive. For instance, a short term (8 days) manipulative experiment conducted with *F. vesiculosus* showed that low salinity slowed down the recovery of growth and photosynthetic performances after an exposure to high water temperature (Takolander et al., 2017b). Interactive effects may occur and are of course important, but, if present, they are included in our combined effect. Further, while our experiment was designed to measure the tolerance of *F. vesiculosus* to the averaged expected changes in seawater conditions, climate change effects will also enhance climate variability (e.g. frequency and intensity of heat and cold waves, Vasseur et al., 2014). For instance, Graiff et al. (2015) showed that *Fucus* is able to acclimate to higher temperature only if there is enough acclimation time.

4.2. Potential of Fucus to adapt to future conditions

The potential for adaptive responses to the predicted future salinity/temperature conditions was indicated by among-individual variation in performance, and, especially by the differential responses of individuals to climate change. The among-individual variation might have different explanations. That we cloned and reared replicated ramets of each individual in common garden conditions entails that the differences we found among clones do represent genetic differences in plasticity. However, a possibility remains that differences among clones include some carry-over effects from the original environment of the sampled individuals, the clonal mothers. It is difficult to judge the relevance of such carry-over effects but even if they contributed to variation detected among individuals (i.e. affect the main effect of individual) we find highly unlikely that they would do differently so in current and future conditions (i.e. affect the individual-by-climate change interaction). Thus, we consider the among-individual variation in responses to climate change to represent genetic variation in reaction norms, i.e. variation in phenotypic plasticity of traits responsible for tolerance. A high degree of such within-population variation in quantitative traits that are closely related to fitness is considered to be the core component of adaptive evolution, allowing the species persistence in a changing environment (Pigliucci, 2005; Wrange et al., 2014).

The observed among-population variation in growth and survival within regions likely indicates variation in tolerance to climate change at a regional spatial scale, within both the entrance and marginal regions of the Baltic Sea. Within the entrance region, all populations survived equally well in current and future salinity/temperature conditions, but *Fucus* from the G population were the most tolerant to future conditions, with the least decrease in growth. The populations from the marginal region differed in their responses to climate change, both in survival and growth. Given the strong spatial genetic structuring (Tatarenkov et al., 2007; Pereyra et al., 2013; Ardehed et al., 2016) and reduced dispersal capacity of Baltic *Fucus* (Serrão et al., 1996b), we consider it likely that such among-population variation within region might represent genetic differentiation in plasticity. Intraspecific geographic variation in tolerance to climate change, such as found here and also in the Atlantic *F. serratus* and *F. vesiculosus* (Pearson et al., 2009; Jueterbock et al., 2014; Saada et al., 2016), means that some populations are more vulnerable than others to climate change. The tolerant populations may provide local persistence assurance through acting as sources for floating thalli that may disperse and generate gene flow over long distances (Röthausler et al., 2015).

Further, the significant individual-by-climate change interaction in growth of entrance and central populations and in survival of marginal populations suggests the existence of genetic variation in phenotypic plasticity. Also other studies have found individual-by-environment -interactions in quantitative traits of *Fucus* indicating genetic variation in plasticity to different environmental conditions, such as growth responses to light or nutrient regimes (Jormalainen and Honkanen, 2004) or phlorotannin responses to herbivory and depth distribution (Jormalainen and Ramsay, 2009). In our study, those individuals from the entrance and central regions that survived in future conditions until the end of the experiment also showed genetic variation in plasticity of growth (individual-by-climate change -interactions), with the variation in growth remaining also in future conditions after mortality. Upon this variation in plasticity, natural selection can alter the reaction norms of growth.

5. Conclusion

Our results imply that the projected increase in temperature and decrease in salinity will be challenging for *Fucus* populations, particularly in the central and marginal regions of the Baltic Sea. There, the abundance of *Fucus* is likely to decline unless populations cannot respond by adaptive evolution of tolerance. Our experiment with almost instant exposure to future conditions represents an extreme scenario. The future conditions we used are a projection for the end of this century (2070–2099) so *Fucus* will be confronted with a gradual change taking place over several generations. We found indications of phenotypic plasticity and genetic variation in tolerance of *Fucus* to the projected future conditions, both within and among the Baltic Sea populations, suggesting potential for adaptive responses exists. Thus, adaptive increase of tolerance may provide persistence in the face of climate change. However, our data just documents the potential for adaptation but does not allow estimations whether the speed of adaptation can match the rate of change. Furthermore, the fate of *Fucus* populations in the Baltic Sea will strongly depend on how the biotic interactions within the entire associated community, such as with the competing macro-and microalgae and grazers, will respond to climate change. Further research on such community responses is needed.

Authors' contributions

VJ, LR and E.R. conceived and designed the experiment. All authors performed the experiment. LR analyzed the data. LR led the writing of the manuscript; all authors contributed to the text.

Conflicts of interest

None.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.marenvres.2017.12.016.

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